

The effect of morphological variation of seagrasses on feedback mechanisms

Abstract

Seagrasses are marine plants that are at the basis of many marine ecosystems. However around the globe seagrasses are in decline. They are ecosystem engineers that shape the conditions of many systems. Seagrasses may create feedbacks by altering systems in such a way that the conditions for seagrass itself increase. Most importantly, seagrasses decrease wave energy and the speed of water flow through the canopy. This increases sedimentation and decreases resuspension of sediment leading to less floating particles and better light conditions. However, the strength of feedback mechanisms may not be the same for every species of seagrass since there are morphological differences. This essay aims to describe the morphological variation among seagrass species and what these variations in morphology mean for the strength of feedback mechanisms. Morphological differences in both above- and below-ground structures are described that will likely affect the strength of feedbacks that are driven by these structures. Water flow and wave energy is likely most attenuated by leaves that are longer, more rigid and have a hydrodynamically disruptive shape. Furthermore, larger seagrasses form a relatively large amount of below-ground biomass causing them to be more effective at stabilizing the sediment also making them more vulnerable to sulphide poisoning. Also, intertidal seagrasses with smaller, narrower leaves are most efficient at reducing desiccation stress and seagrasses with roots and rhizomes that reach deep and branch often have the strongest protection against uprooting. If the species composition of seagrass meadows change in the future, the strength of feedback mechanisms may change as well.

Table of contents

Table of contents.....	2
Introduction.....	3
The morphology of seagrass species.....	4
Above-ground variation	4
Stems	5
Leaves	5
Below-ground variation.....	6
Rhizomes	6
Roots.....	6
Feedback mechanisms of seagrasses	7
Above-ground seagrass feedback mechanisms	8
Improved light conditions and nutrient supply.....	8
Self-organised spatial patterns.....	9
Desiccation reduction.....	9
Feedback mechanisms at interface above- and below-ground	10
Sediment stabilization	10
Changing sediment grain size.....	10
Below-ground feedback mechanisms	11
Sulphide toxicity	11
Protection from uprooting	11
Conclusions.....	11
Implications for seagrasses in the future	12
References.....	13

Introduction

Seagrasses are underwater flowering plants that perform important ecosystem services in marine systems across the globe. They are herbaceous plants that can form large meadows, growing in areas ranging from intertidal to deeper offshore areas of up to 61 meters deep (Macreadie et al., 2017).

Seagrasses are often the main primary producer of marine systems that support the rest of the system by producing organic matter. Seagrass meadows are also a habitat for many species and provide food for megaherbivores such as manatees, dugongs and green sea turtles. Furthermore they stabilise sediments and cycle nutrients (Orth et al., 2006; Short et al., 2011; Unsworth & Coles, 2014). Many ecosystem services provided by seagrasses are important to humans. For example, seagrass meadows are nursery grounds for some of the most economically interesting marine species that live in deep water habitats (Macreadie et al., 2017; Unsworth & Cullen, 2010) and the various fish and invertebrate species that live in seagrass meadows are relied upon by many small and large scale fisheries (Short et al., 2011; Unsworth & Cullen, 2010). Also, large amounts of plant material, organic matter and animal biomass are produced in seagrass meadows and are exported to surrounding systems, supporting these systems. The small-scale fisheries that fish in these surrounding systems are therefore also relying on seagrasses (Unsworth et al., 2018). Another important ecosystem function is that seagrasses act as a carbon sink, they are estimated to account for 10 to 18 percent of the oceanic carbon uptake (Kennedy et al., 2010). Seagrasses can capture carbon as biomass at much faster rates than terrestrial forests and can store this carbon for very long periods of time (Macreadie et al., 2014).

The amount of seagrass is declining worldwide. According to Waycott et al. (2009) 110 km² of seagrass has disappeared yearly since 1980, with a total loss of 29% of the total seagrass area. This rate of loss is accelerating and places seagrasses as one of the most threatened ecosystems on the planet. Many seagrass meadows are dominated by a single species, making them vulnerable for diseases that can decrease their numbers significantly (Waycott et al., 2009). Other direct causes of seagrass loss are coastal engineering, fishery, boat propellers, cyclones and tsunamis (Short & Wyllie-Echeverria, 1996; Unsworth & Coles, 2014; Waycott et al., 2009). Besides direct causes, indirect causes of seagrass loss may be even more damaging (Waycott et al., 2009). For example, seagrasses are highly dependent on light availability which makes them vulnerable to environmental changes (Collier et al., 2016; Duarte, 1991b; Orth et al., 2006). Higher nutrient addition and sediment runoff caused by humans decreases the water quality. Besides that, overfishing decreases the amount of predators, this cascades down the food web resulting in less herbivores that clean the seagrass of epiphytes. This in turn makes growth conditions for seagrass worse. Invasive species have also been found to negatively affect seagrass meadows (Orth et al., 2006; Waycott et al., 2009) and global warming through climate change will also likely negatively affect seagrasses (Orth et al., 2006; Unsworth & Coles, 2014).

A further loss of seagrass will decrease the flow of energy from seagrass meadows to surrounding ecosystems. Many species that depend on seagrass for their habitat or nursery grounds will be threatened. Carbon sequestration, biomass production and nutrient cycling will also decrease (Waycott et al., 2009). Seagrass meadows may even turn from carbon sinks into carbon sources (Macreadie et al., 2014). It is clear that seagrasses are at the basis of many marine systems upon which humans rely and the protection and conservation of seagrasses is vital for preserving these systems.

In order to prevent further seagrass decline it is important to understand the interactions between seagrasses and their environment. Some of these interactions result in feedback loops where

seagrasses increase or decrease the suitability of the environment for more seagrass to grow. The decrease of seagrass meadows means that these feedback mechanisms become weaker with generally negative consequences for seagrass growth as a result. This may ultimately result in an alternative stable state where less seagrass is present (Maxwell et al., 2017).

Besides the decline in seagrass abundance, the species composition of existing meadows may change and seagrass species diversity may decline (Maxwell et al., 2017). Short et al. (2011) describes 72 species of seagrass in six families, of which 10 species (14% of total) are listed as endangered. Among these seagrass species there is morphological variation and structures of the plant can be shaped differently (Macreadie et al., 2017). Because of this, not all seagrasses may interact with their environment in the same way. If this is the case then the strength of feedback mechanisms may be different between species with varying morphologies.

To investigate this, this essay aims to determine how the strength of feedbacks depends on morphological traits of seagrass species. This is investigated by using information from the scientific literature to answer four sub questions: (1) How do seagrass species vary morphologically above-ground? (2) How do seagrass species vary morphologically below-ground? (3) How does above-ground morphology affect feedbacks? (4) How does below-ground morphology affect feedbacks?

Improving our knowledge of the effects of morphology on feedback mechanisms will help us to anticipate how these feedback mechanisms will change if seagrass species diversity declines or if the species compositions of seagrass meadows change. This knowledge may help seagrass conservation or restoration efforts.

The morphology of seagrass species

All seagrass species share a common structure of stems, sheaths and leaves above ground and roots and rhizomes below ground (Macreadie et al., 2017). However, within this structure there is variation.

Above-ground variation

As depicted in figure 1, several morphological groups of seagrasses can be identified:

1. Plants with a pair of petiolate leaves on the rhizome node or with leaflets on an erect stem. The leaves are not strap-shaped. This group consists only of *Halophila*, the genus with the smallest leaves ranging from 1cm to 20cm long (Kuo & den Hartog, 2006).
2. Plants with a stem that branches many times. The stem is leafless at the bottom but dense webs of leaf clusters with 5 to 10 leaves are formed higher up (Verduin & Backhaus, 2000), creating a bush like structure. This group only contains the genus *Amphibolis*.
3. Plants with an erect stem and strap-shaped leaves growing from the top of the stem. Includes the genus *Thalassia* of the Hydrocharitaceae and all genera of the Cymodoceaceae except for *Amphibolis*.
4. Plants with no visible erect stem, strap-shaped leaves grow from rhizome nodes. The genus *Enhalus* of the Hydrocharitaceae and all genera of the Posidoniaceae and Zosteraceae belong to this group (Kuo & den Hartog, 2006; Macreadie et al., 2017).

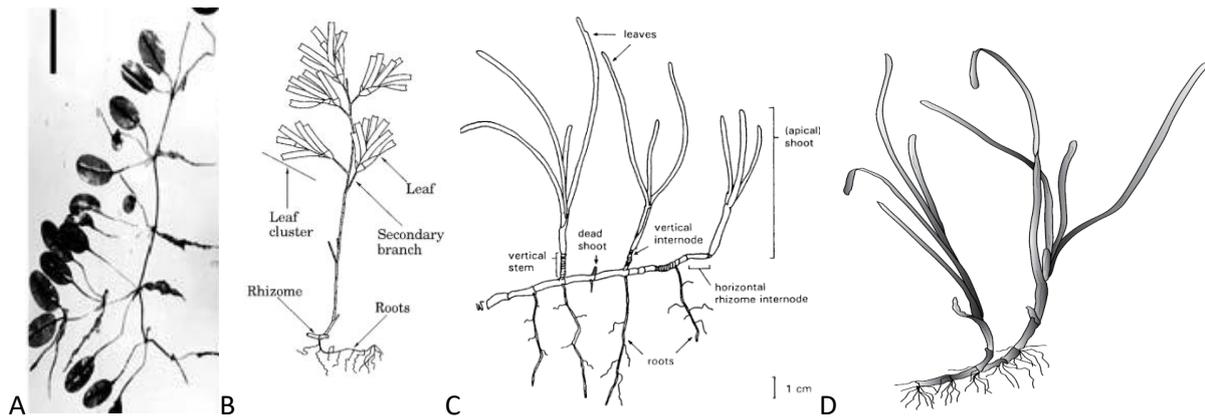


Figure 1: Plant structures of A: *Halophila* (Kuo & den Hartog, 2006), B: *Amphibolis* (Verduin & Backhaus, 2000), C: *Cymodocea* (Vermaat et al., 1997) and D: *Zostera* (Greve & Binzer, 2004).

Furthermore, seagrasses can be divided into small ephemeral species with high biomass production and turnover but low standing biomass (*Halophila*) or larger slower growing species (*Amphibolis*, *Phyllospadix*, *Posidonia*) that have lower overall production and turnover (Macreadie et al., 2017).

Stems

Seagrasses grow erect stems that are formed at the nodes of the rhizomes. Most seagrasses grow rigid stems, however *Syringodium* and a majority of *Halophila* species have softer stems. The stems are often not very branched and can have different lengths depending on the seagrass species (Kuo & den Hartog, 2006). As described earlier, the stems of *Amphibolis* show more branching (Verduin & Backhaus, 2000) while other seagrass species do not grow a stem at all (Kuo & den Hartog, 2006; Macreadie et al., 2017; Vermaat et al., 1997).

Leaves

Seagrass leaves grow either on top of the stems or on the top side of the rhizome at the rhizome nodes in the absence of a stem (Kuo & den Hartog, 2006; Tomlinson & Vargo, 1966). The leaves consist of a leaf sheath at the base and a leaf blade at the end. The function of the leaf sheath is to provide protection for developing leaves and the apical meristem. The leaf blade is where photosynthesis takes place. All seagrasses have strap-shaped leaves except for *Halophila*, which has petiolate leaves or leaflets, and *Syringodium* which has subulate leaves (den Hartog, 1967; Kuo & den Hartog, 2006; Vermaat et al., 1997). The strap-shaped leaves of *Amphibolis* grow in bundles at the top of every branch of its stem but only grow to about 5cm in length (Verduin & Backhaus, 2000). There may also be other differences in leaf shape between strap-shaped seagrass species, for example the leaves of *Posidonia australis* are strap-shaped and flat while the leaves of *Posidonia sinuosa* are also strap-shaped but curved (Trautman & Borowitzka, 1999).

Another difference in leaf anatomy between seagrass genera is the presence or absence of fibre cells in the leaf blades. Fibre cells are cells with thicker but not lignified cell walls that form strands of fibre through the leaf, mostly near leaf margins, vascular bundles and around air lacunae in for example *Posidonia* (Cambridge & Kuo, 1982; Kuo & den Hartog, 2006). This provides the leaves with enough strength to endure strong waves without losing too much flexibility. Fibre strands are not present in every seagrass. All genera of *Cymodoceaceae* except for *Cymodocea* lack fibre cells. *Halophila*, *Ruppia* and *Lepilaena* have reduced fibre cells. Many of the seagrass species with no or few fibre strands are either found in sheltered areas where the water is relatively calm or have very thin leaves on the tip of very long and flexible stems, making fibre strands unnecessary (Kuo & den Hartog, 2006).

Below-ground variation

Rhizomes

Below ground there are also morphological variations between seagrasses. Seagrass rhizomes for example come in a variety of forms. The rhizome is used for several functions such as storing nutrients, anchoring to the substrate, vegetative growth and mechanical support. Most seagrasses that live on either muddy or sandy soils have rhizomes that are herbaceous and have a cylindrical or laterally compressed shape. These rhizomes usually branch monopodially or without a regular pattern. However there are seagrass species that grow on harder soils. For example *Phyllospadix* grows on rocky substrates, the epidermal layers of *Phyllospadix* rhizomes are thicker and serve to strengthen the plant (Cooper & McRoy, 1988). *Amphibolis* and *Thalassodendron* also grow on rocky substrates or on harder sediments, the morphology of their rhizomes is different in that their rhizomes branch sympodially and eventually turn woody.

Except for some species of *Phyllospadix* and *Thalassodendron* all seagrass rhizomes are buried in the substrate (Kuo & den Hartog, 2006; Macreadie et al., 2017). The height of this substrate may increase as a result of sedimentation. To avoid being buried many seagrass species grow vertical rhizomes. The growth rate of these vertical rhizomes is often slower than horizontal rhizome growth and there are strong differences in the amount of branching in vertical rhizomes. The vertical rhizomes of some seagrasses even reach above the sediment (Marbà, 1998).

In general the amount of biomass from seagrass plants is evenly divided between above-ground and below-ground biomass. However this is species specific and though rhizome growth is slower in larger, longer lived seagrasses (Vermaat et al., 1997), these larger species tend to produce thicker rhizomes and higher amounts of below-ground biomass than smaller species (Duarte, 1991a; Duarte & Chiscano, 1999). Larger species also tend to extend their rhizomes deeper in the sediment (Duarte et al., 1998).

Roots

Like stems or leaves, the roots of seagrasses also grow from the nodes between rhizome segments but on the bottom side of the rhizome (Kuo & den Hartog, 2006; Tomlinson & Vargo, 1966; Vermaat et al., 1997). Seagrasses can be found on a variety of substrates. On soft muddy soil *Enhalus* grows large, soft and unbranched roots with small root hairs. *Zostera* grows on muddy soils and also on sandy soils. *Zostera* forms roots that are unbranched as well and are always formed in two groups of 2 – 12, unlike *Enhalus* each root has long root hairs. Like *Zostera*, *Thalassia* and *Halophila* form unbranched roots with large root hairs but these roots are not formed in two groups. *Thalassia* and *Halophila* grow on a range of substrates. On coral sands, *Syringodium*, *Cymodocea* and *Halodule* roots are branched without many root hairs. The roots of *Amphibolis* are very branched and even completely lack root hairs. *Thalassodendron* has large, sturdy wooden roots with root hairs only at the tip of the root. *Amphibolis* and *Thalassodendron* are both found on hard sediments and rocky substrata (Kuo & den Hartog, 2006). *Posidonia* has thick and very branched roots and also has root hairs. Though often found on sandy soils (Kuo & den Hartog, 2006) *Posidonia* can also be found on rocky substrates where the sticky root hairs allow it to attach to the surface (Badalamenti et al., 2015). The genus *Phyllospadix* is also commonly found on rocky surfaces and in conditions of strong water currents (Cooper & McRoy, 1988). Similar to *Zostera*, the roots of *Phyllospadix* also grow in two groups. However these roots are very short and have a high concentration of root hairs like *Posidonia* (Kuo & den Hartog, 2006).

Besides the substrate seagrasses grow on, the size of the seagrass is also important for root morphology. Duarte et al. (1998) found that bigger seagrass species have thicker roots. These thick

roots have large air lacunae for transporting oxygen from photosynthetic parts of the plant to the roots. In contrast to root thickness, root length does not seem to be predicted by the size of the seagrass but by other factors such as nutrient limitation or the need for anchoring (Duarte et al., 1998). The thinner roots of smaller species are likely more suitable for efficient nutrient uptake (Duarte et al., 1998) while the roots of larger species are often located in deeper sediment layers. This gives larger species the ability to utilize nutrients that are buried deep in the sediment, making them less dependent on nutrient inputs than smaller species (Duarte, 1991a; Duarte et al., 1998).

Feedback mechanisms of seagrasses

Seagrasses interact with their environment in such a way that they alter the conditions of their environment. This can happen in various ways and can have both beneficial and detrimental consequences for the seagrass itself, creating positive and negative feedback mechanisms (Maxwell et al., 2017). Table 1 gives an overview of feedbacks that are driven by above- or below-ground structures of the seagrass plant. The effects of morphological differences in these above- and below-ground structures on the feedback mechanisms are also described.

Table 1. Above- or below-ground feedback mechanisms driven by seagrass (Maxwell et al., 2017).

Location	Feedback name	Description
Above-ground	Improved light conditions	Seagrasses attenuate waves and water flow in their canopy, leading to increased sedimentation. The increased sedimentation reduces floating particles in the water column and thereby improves the light conditions (Bradley & Houser, 2009; van der Heide et al., 2011).
	Increased nutrient supply	The increased sedimentation caused by seagrass leads to larger amounts of nutrients reaching the sediment and becoming available for the seagrass (Folmer et al., 2012; van Katwijk et al., 2010).
	Self-organised spatial patterns	Turbulence around seagrass shoots increases further into the meadow. This causes sediment erosion and may decrease growth conditions for seagrass leading to self-organised spatial patterns (Maxwell et al., 2017; van der Heide et al., 2010a).
	Desiccation reduction	In intertidal areas seagrasses can hold water above the water level, decreasing desiccation stress and improving conditions for seagrass growth (Shafer et al., 2007; Tsai et al., 2010).
Interface above- and below-ground	Sediment stabilization	Above-ground, seagrasses stabilize the sediment by reducing wave action and water flow velocities (Fonseca & Cahalan, 1992; Fonseca & Fisher, 1986; Gacia & Duarte, 2001). Below-ground, seagrass roots and rhizomes hold the sediment in place and thus improve the conditions for seagrass to grow (Duarte et al., 1998; Luhar et al., 2008; Rattanachot & Prathep, 2015).
	Changing sediment grain size	If sedimentation and sediment stability increase, the sediment grain size becomes smaller. If sediment conditions decrease then the grain size becomes larger (Christianen et al., 2013; Maxwell et al., 2017; van Katwijk et al., 2010).
Below-ground	Sulphide toxicity	Increased sedimentation may lead to anoxic conditions in the sediment where sulphide concentrations may increase. This may negatively affect seagrass growth (Folmer et al., 2012).
	Protection from uprooting	Increasing amounts of seagrass roots and rhizomes offer more protection from uprooting (van der Heide et al., 2010a).

Above-ground seagrass feedback mechanisms

Improved light conditions and nutrient supply

Seagrass leaves and stems improve the growth conditions for seagrasses by reducing the energy of waves and of water currents that flow through the meadow canopy (Bradley & Houser, 2009; Fonseca & Cahalan, 1992). This increases sedimentation rates and results in improved light conditions because there are less floating particles in the water column. The result is a positive feedback mechanism (Bradley & Houser, 2009; van der Heide et al., 2011). According to de Boer (2007) this feedback is the most important of all feedbacks because seagrasses are very light dependent. If light conditions improve, growth conditions for seagrasses improve as well. The increased sedimentation also results in more organic matter being deposited in the sediment. This organic matter increases the amount of nutrients available for the seagrass and thereby also improves seagrass growth conditions (Folmer et al., 2012; van Katwijk et al., 2010). Both feedbacks are described in figure 2.

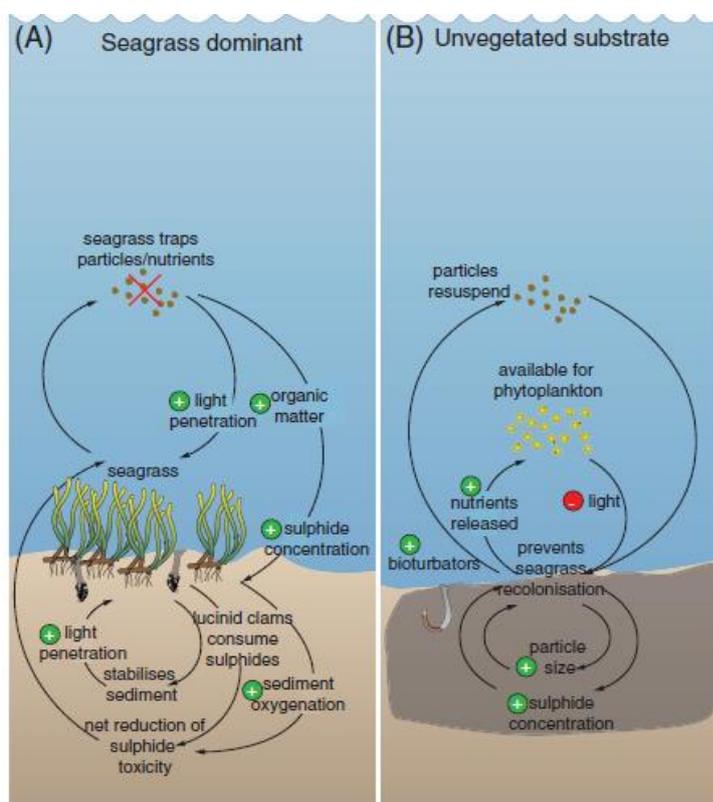


Figure 2. Seagrass feedback mechanisms with sediment and light conditions (Maxwell et al., 2017).

The capacity of seagrasses to reduce wave strength and water flow velocities in the canopy may not be the same for seagrass species with varying leaf and stem morphologies. Consequently, the light condition and nutrient supply feedback mechanisms may be stronger in some species than in others. Fonseca & Cahalan (1992) investigated the wave attenuating effect of *Halodule wrightii*, *Syringodium filiforme*, *Thalassia testudinum* and *Zostera marina*. They found that the length of the leaf in relation to the depth of the water is an important aspect for wave attenuation by seagrass leaves. As soon as the water depth becomes larger than the leaf length, wave attenuation decreases. Leaf length and water depth are therefore important factors for wave attenuation (Fonseca & Cahalan, 1992).

Despite finding differences in leaf shape no considerable difference in wave attenuation was found between the investigated species (Fonseca & Cahalan, 1992). However for unidirectional water flow such a difference has been found in a previous study. The strap-shaped leaves of *H. wrightii*, *T.*

testudinum and *Z. marina* caused higher flow reductions than the more hydrodynamically smooth cylindrical leaves of *S. filiforme* (Fonseca & Fisher, 1986). This suggests that the shape of the leaves does not necessarily impact wave attenuation by seagrasses but has an effect on the reduction of water flow speeds through the canopy. Furthermore, the rigidity of the plant plays a role as well. Fibre strands in seagrass leaves increase rigidity (Kuo & den Hartog, 2006) and this increases the drag created by seagrass plants (Bouma et al., 2005; Bradley & Houser, 2009). Seagrasses with longer leaves that are more rigid and have are shaped less hydrodynamically are therefore likely to create a larger increase in sedimentation and consequently drive stronger light condition and nutrient supply feedbacks.

However, water flow is only reduced if the vegetation density is sufficient. Bouma et al. (2009) found that scale-dependent feedbacks in the salt marsh species *Spartina anglica* are density dependent. This is also true for seagrass. The drag created by seagrass causes a water flow attenuation only if seagrass density is sufficiently high, in areas of low seagrass density or around the edges of seagrass meadows they cause increased turbulence. This turbulence leads to sediment resuspension into the water and sediment erosion (Bouma et al., 2009; Luhar et al., 2008). Thus, seagrass growth is promoted in areas where seagrass is already present and reduced in areas without a sufficient amount of seagrass. This way, the existing distribution of vegetation is maintained (Luhar et al., 2008). Some researchers report that for the attenuating effect of seagrass on water flow the density of seagrass meadows may be more important than morphology (Bradley & Houser, 2009; van Katwijk et al., 2010).

Self-organised spatial patterns

Although in a lesser degree than in sparse meadows, seagrass shoots in dense meadows also create turbulence in the water flowing around it. This turbulence increases with further distance into the seagrass meadow and causes sediment erosion around seagrass shoots that are situated further inside the meadow (van der Heide et al., 2010a). In some cases this could limit the size of seagrass meadows leading to self-organised spatial patterns (Maxwell et al., 2017; van der Heide et al., 2010a). This effect increases if water flow velocities are high but may be absent in systems where water flow velocities are relatively low. (Bouma et al., 2009). This feedback is also likely stronger in seagrasses that are most effective at attenuating water flow in their canopy.

Desiccation reduction

Seagrasses also drive a feedback mechanism in intertidal areas. Most seagrass species do not occur in the intertidal area because they are not able to withstand the desiccating conditions at low tide. However some species do tolerate desiccation and these species can be found in the intertidal area, for example *Z. marina*, *Zostera japonica* and *Zostera novazelandica* in temperate regions and *Halodule uninervis*, *H. wrightii*, *Halophila ovalis*, *Cymodocea rotundata*, *Thalassia hemprichii* and *Enhalus acoroides* in tropical regions (Powell & Schaffner, 1991; Shafer et al., 2007).

The photosynthetic capacity of these seagrasses decreases when desiccation occurs during low tide. However, seagrass leaves retain water above the water level during dry conditions (Powell & Schaffner, 1991). This retention of water by seagrass reduces desiccation stress during low tide, improving conditions for seagrass growth and thus creating a positive feedback (Shafer et al., 2007; Tsai et al., 2010). Desiccation stress has been found to be more severe for upper intertidal species (for example *Z. japonica*) than for species that grow in lower intertidal or subtidal areas (for example *Z. marina*). The main cause for this is likely that plants from the upper tidal area tend to have smaller and narrower leaves that overlap to offer each other shade and are capable of lying flat on the wet sand during low tide (Shafer et al., 2007; van Katwijk et al., 2010). Seagrasses with smaller and

narrower leaves are therefore more effective at decreasing desiccation and create a stronger positive feedback.

Feedback mechanisms at interface above- and below-ground

Sediment stabilization

Besides increasing sedimentation, the reduced waves and water flow in the canopy enhance sediment stability as well, see figure 2 (Fonseca & Fisher, 1986). Stable sediments have a lower sediment resuspension rate which has a positive effect on seagrass growth (Luhar et al., 2008). Sediment stabilisation happens both directly (Fonseca & Cahalan, 1992; Gacia & Duarte, 2001) and indirectly by allowing benthic microalgae (diatoms) and cyanobacteria to develop biofilms on the sediment that offer further stabilization (Folmer et al., 2012).

Besides seagrass stems and leaves, the roots and rhizomes also have a stabilizing effect on the sediment by forming a dense web of belowground structures that hold the sediment in position (Duarte et al., 1998; Rattanachot & Prathep, 2015). This way they decrease the erodibility of the sediment by increasing the force needed to resuspend sediment from the sea floor. If the density of below-ground structures increases, the stabilizing effect on the sediment increases as well (Maxwell et al., 2017). Larger seagrass species tend to have more below-ground biomass (Duarte & Chiscano, 1999) and are therefore likely to have a larger stabilizing effect on the sediment and drive a stronger feedback than smaller species. The smaller seagrass *Halophila decipiens* was found to have a similar stabilizing effect on the sediment, possibly because its leaves and rhizomes are located closer to the sediment. However *H. decipiens* is an opportunistic species that can only thrive in a narrow range of conditions. (Fonseca, 1989).

Some seagrass species such as *Posidonia oceanica* and *Thalassodendron ciliatum* can form very dense mats out of their rhizomes and the remains of roots and leaf sheaths. These mats can be several meters thick and can act as a substrate to form reefs on which new seagrasses can grow. These mats can remain in place and thus stabilize the sediment in its interstices for long periods of time (Duarte & Chiscano, 1999; Duarte et al., 1998; Kuo & den Hartog, 2006; Tomlinson & Vargo, 1966).

Changing sediment grain size

The increased sedimentation within meadows causes sediment grain size to become smaller. Conversely, sediment around meadow edges or in sparser meadows becomes coarser because of resuspension of the fine sediment as a result of increased turbulence (van Katwijk et al., 2010). Similarly, the roots and rhizomes of seagrasses reduce sediment resuspension in denser seagrass meadows but not in sparse meadows or outside meadows. As a result, the sediment grain size becomes smaller within seagrass meadows and larger outside (Christianen et al., 2013; Maxwell et al., 2017). The resulting muddification and sandification may create feedbacks depending on the state of the system. If the system is sandy muddification will increase nutrient supply which improves conditions for seagrasses to grow. On the other hand, if the system becomes too muddy the sediment can become anoxic. In this case sandification can alleviate this by increasing the oxygen supply to the sediment (van Katwijk et al., 2010). Since the changing sediment size feedback is partly driven by the effects of the seagrass plant on waves and water flow, it can be expected to be the strongest for seagrasses with long, rigid and hydrodynamically disrupting leaves. Seagrass roots and rhizomes also play an important role, the feedback is likely stronger in larger seagrass species that tend to grow relatively large amounts of below-ground biomass.

Below-ground feedback mechanisms

Sulphide toxicity

If sedimentation increases so much that the concentration of organic matter in the sediment becomes too high then the microbial breakdown of the organic matter may create anaerobic conditions in which toxic sulphide is formed (Folmer et al., 2012). This sulphide can be detoxified by oxidizing it, creating sulphate which is harmless (Greve & Binzer, 2004; van der Heide et al., 2010b). However, if the water flow velocities and sediment grain size decrease then the oxygen supply to the sediment decreases as well. As a result less sulphide can be oxidized, creating a negative feedback (Folmer et al., 2012).

As described in figure 2, seagrasses can protect themselves from high sulphide concentrations by saturating their roots and the sediment with oxygen. This causes the sulphide to react with the oxygen before it can reach the root tissue (Greve & Binzer, 2004). Seagrasses need a constant supply of oxygen to be able to do this, which is provided by photosynthesis during daytime (Borum et al., 2005) and transported to the roots by air lacunae (Duarte et al., 1998). However at night the plants are not able to produce oxygen and are dependent on the oxygen supply of the surrounding water, this is often insufficient to provide adequate protection (Borum et al., 2005). If there is insufficient oxygen in the water column the oxygen supplies in the below-ground biomass will eventually run out. Sulphide can then invade the plant tissue and damage the plant (Borum et al., 2005). The decreased supply of oxygen to the sediment caused by increased sedimentation therefore causes dense seagrass meadows to become more vulnerable to sulphide invasion at night. The amount of below-ground biomass in denser seagrass meadows is also larger, increasing their vulnerability to sulphide invasion further (Borum et al., 2005; Greve & Binzer, 2004). Similarly, larger seagrass species may be more susceptible to sulphide invasion because they develop a relatively large amount of below-ground biomass compared to above-ground biomass that is photosynthetic (Hall et al., 1999).

Toxic sulphide levels can be reduced by lucinid bivalves that house bacteria that oxidize sulphide. Seagrasses engage in mutualistic interactions with these bivalves by increasing the amount of oxygen and organic matter that is available for the bivalves. In return the bacteria in the bivalves reduce sulphide levels, improving the conditions for seagrass growth (van der Heide et al., 2012).

Protection from uprooting

Rhizomes and roots anchor the seagrass plant in the sediment and protect it from uprooting. This effect becomes stronger when seagrass density increases. The result is a positive feedback where seagrasses in higher densities become less vulnerable to uprooting when the sediment is disturbed (van der Heide et al., 2010a). Besides that, roots that reach deeper and branch more are more effective at preventing uprooting (Balestri et al., 2015). Larger seagrass species tend to have deeper rhizomes and roots that further penetrate the sediment (Duarte et al., 1998), they are therefore likely more effective against uprooting.

Conclusions

The morphology of above- or below-ground structures of the seagrass plant are likely to affect the strength of feedback mechanisms in the following ways:

- The capacity of seagrasses to attenuate water flow through the canopy is likely the strongest when seagrass leaves are longer, more rigid and more hydrodynamically disruptive (Bouma et al., 2005; Fonseca & Cahalan, 1992; Fonseca & Fisher, 1986). This means that the improvement of light conditions, increase of nutrient supply and stabilization of the sediment by increasing seagrass densities is stronger for seagrasses with these traits. These

feedbacks can be positive or negative depending on seagrass density (Bouma et al., 2005; Luhar et al., 2008).

- Similarly, self-organised spatial patterns are also most likely to emerge in seagrasses that are most effective at attenuating water flow.
- Intertidal seagrasses with smaller and narrower leaves are more effective at reducing desiccation (Shafer et al., 2007; van Katwijk et al., 2010).
- Besides attenuation of waves and water flow, sediment stability is also increased by below-ground structures. Larger seagrass species grow relatively more below-ground biomass (Duarte & Chiscano, 1999) and therefore are likely to create a stronger sediment stabilizing feedback.
- Their relatively high levels of below-ground biomass makes larger seagrasses more susceptible to sulphide invasion (Hall et al., 1999).
- Roots and rhizomes that reach deeper in the sediment and branch extensively offer the most effective protection against uprooting (Balestri et al., 2015). The roots and rhizomes of larger seagrasses often reach deeper (Duarte et al., 1998) and are therefore likely the most effective.

Implications for seagrasses in the future

Seagrasses are currently in decline across the globe (Waycott et al., 2009) and the species composition of many seagrass meadows may change. In seagrass meadows in southern Florida for example Hall et al. (1999) found a decrease in the distribution of *H. wrightii* and *S. filiforme* but not *T. testudinum*. On the other hand, in north-western Florida *T. testudinum* distribution decreased while *H. wrightii* and *S. filiforme* increased in distribution (Hale et al., 2004). Although these studies show different results, they both indicate that the species composition of seagrass meadows are changing.

If *S. filiforme* increases the strength of the light improvement and sediment stabilisation feedbacks by the seagrass meadow would decrease because the cylindrical leaves of *S. filiforme* are less effective at reducing current speeds (Fonseca & Cahalan, 1992). If *T. testudinum* increases the sediment would likely become more stable because of high amounts of below-ground biomass. However, this higher amount of below-ground biomass may also make *T. testudinum* more vulnerable to sulphide invasion. This would mean that sediment sulphide toxicity would become more common if *T. testudinum* increases, the frequent die-offs seen in *T. testudinum* meadows may be caused by this (Hall et al., 1999).

In the Caribbean, the invasive seagrass *Halophila stipulacea* is expanding at a very fast rate at the cost of the native *T. testudinum*. Originating in the Indian ocean, *H. stipulacea* is capable of fast clonal growth and detached fragments of the plant can quickly disperse to new areas and colonize them. *H. stipulacea* is therefore effective at colonizing bare spots in native seagrass meadows caused by disturbance events. The replacement of the larger *T. testudinum* by the smaller *H. stipulacea* will likely affect feedback mechanisms, *H. stipulacea* has smaller leaves and thus has a smaller attenuating effect on waves and water flow. Besides that, it also has less below-ground biomass. This means that *H. stipulacea* will likely be less effective at stabilizing the sediment and improving light conditions. On the other hand, *H. stipulacea* has also colonized areas where previously no seagrasses were found, increasing the strength of feedback mechanisms in those areas. Furthermore, in the Mediterranean sea where *H. stipulacea* is also non-native it did not negatively impact the local native species (Smulders et al., 2017).

Similar changes in species composition may occur in seagrass meadows across the globe with possible consequences for the strength of feedback mechanisms in these systems. Though feedbacks

are likely density dependent, understanding the effect of morphology on the strength of feedback mechanisms may help to improve efforts to protect or restore seagrass meadows.

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